

THE INTERRELATIONSHIP OF EARLY COLONY DEVELOPMENT, MONTICULES AND BRANCHES IN PALAEOZOIC BRYOZOANS

by MARK E. PODELL *and* ROBERT L. ANSTEY

ABSTRACT. The generalized early colony development of Ordovician trepostome bryozoans includes two distinct stages: an earlier triangular colony, or protoecial cone, followed by a later circular colony, or ancestrular disc, in which vestiges of the protoecial cone are observable. Monticules, polymorphic zooid clusters characteristic of later astogeny, reproduce the structure of the zone of early development, including a replicate of the ancestrula, the monarchozooid. A second type of ancestrular replicate, the basilozooid, is found within the axial zones of colony branches. The evidence from colony structure and zooid morphology is here interpreted as illustrating the presence of a growth regulator. It is inferred that the ancestrula and its replicates, monarchozooids and basilozooids, exerted local dominance over their respective regions of the colony, and that this is reflected in radial zooid alignments and gradients in zoecial size. A colony in which several monticules were destroyed by borings shows disruption of normal zoecial alignments in the areas affected. The programme of early development is repeated many times, with modifications, to produce all the later stages of colony growth.

THE early stages of colony development in Palaeozoic bryozoans are inadequately known. Cumings (1904, 1905) compared the early astogeny of the Palaeozoic Fenestellidae and Palescharidae with that of Recent bryozoans. In his study of the early development of several genera (1912), he firmly established the bryozoan affinity of the Order Trepostomata. Borg (1965) briefly compared the early colony development of the Palaeozoic genus *Prasopora* to that of modern cyclostomes. Corneliussen and Perry (1973) compared the initial region of the Silurian trepostome *Hallopora elegantula* with that of the Ordovician *H. dalei* figured by Cumings. Boardman and McKinney (1976) provided a detailed comparison of the Palaeozoic trepostome *Rhombotrypa* with that of Recent lichenoporiid cyclostomes described by Harmer (1896) and Borg (1926, 1933). In addition, McKinney (1977a, 1977b, 1978) has incorporated early colony development into his over-all studies of the functional morphology of Palaeozoic lyre-shaped fenestellids and paraboloid-based trepostomes. The present paper illustrates additional details of early colony development in a variety of Ordovician trepostomes, based upon scanning electron micrographs of important developmental stages, and also attempts to show that the early developmental stages, in slightly modified form, are reproduced repeatedly in later stages of colony growth.

Urbanek's work (1960, 1973, reviewed by Gould 1977) on morphogenetic gradients in graptolite colonies and their phylogenetic modifications provides a possible example of how a growth regulator, analogous to auxins in plants, can be documented in the fossil record by means of 'natural experiments' on damaged and regenerated colonies. This paper illustrates an analogous situation in a bryozoan colony in which normal growth patterns have been disrupted in a damaged area. In reference to Urbanek's work, however, Boardman and Cheetham (1973) concluded that a morphogenetic substance produced by the primary zooids of a bryozoan colony could not have been

continuously diffused throughout all of colony growth, primarily because of the limited size, apparently brief duration, and possible early isolation of a colony's initial region. The present study illustrates, however, that the colony's founder zooid is regularly reproduced at multiple locations throughout all stages of colony growth, and infers that any morphogenetic activity carried out by the founder zooid was likewise reproduced by all of these secondary founders, or monarchic zooids.

Morphogenetic gradients around budding sites in an Ordovician bryozoan colony were mapped by Anstey *et al.* (1976), who inferred from them the activity of a morphogenetic substance comparable with that described by Urbanek. Analogously located physiologic gradients were measured in living cheilostome bryozoans by Bronstein (1939). In addition, Dzik (1975) inferred that trends in cheilostome phylogeny reflected the modification of morphoregulatory substances produced by the ancestrula. This study illustrates the details, using scanning electron microscopy, of the monarchic zooids found at the origin of morphogenetic gradients in later stages of the same colonies in which early development was also analysed. Some preliminary details of this work have been presented in abstract form by Anstey and Pachut (1977).

MATERIALS AND METHODS

All previous studies of early colony development in Palaeozoic bryozoans have been entirely based upon light microscopy. This study emphasizes the use of scanning electron microscopy (using an ISI Super III) to illustrate the details of all stages of colony development, based on both external colony surfaces and etched serial polished sections. Scanning electron micrographs provide better resolution of both skeletal wall structure and external morphology, especially of minute colonies, than that possible with light microscopy.

Specimen materials include 120 zoaria or brachiopod shells on which multiple zoaria were encrusted, of Middle and Late Ordovician age from Minnesota and the Ohio Valley. All specimens were ultrasonically cleaned and 'sputter' coated with gold prior to microscopy. Polished sections were etched with formic acid for 5 to 10 seconds. All micrographs were prepared at a standard beam orientation of 90 degrees to the microscope stage, thereby eliminating distortion due to foreshortening.

All specimens illustrated are in the collections of Michigan State University (MSU) and Indiana University.

EXPLANATION OF PLATE 126

Plates 126-129 are all photographs taken with the scanning electron microscope.

Fig. 1. Trepostome protoecium. MSU 220314-00024a. Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 360$.

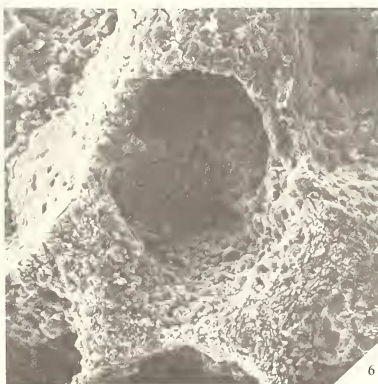
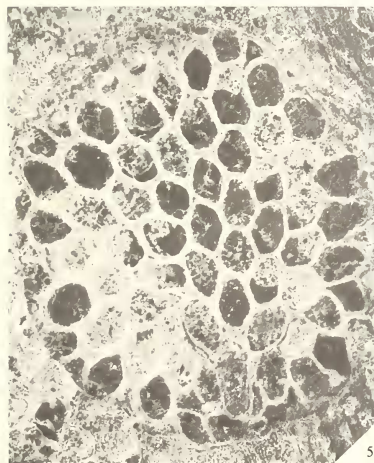
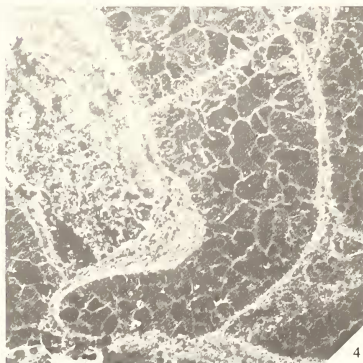
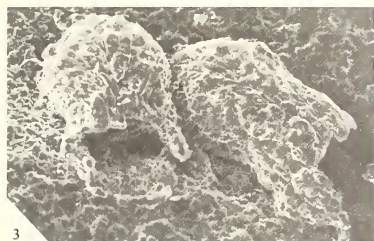
Fig. 2. Trepostome protoecium. MSU 220314-00024a. Enlargement of upper right-hand portion of fig. 1, rotated 90° to the left, illustrating elongate crystal units with sutured margins, Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 2400$.

Fig. 3. Trepostome protoecia. MSU 220314-00024b. Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 180$.

Fig. 4. *Hallopora* sp. MSU 220314-00090. Longitudinal section through the protoecium, ancestrula, and associated thickened backwall, Madison, Indiana, Dillsboro Formation (Late Ordovician), $\times 200$.

Fig. 5. *Amplexopora*? sp. MSU 220314-00027a. Transverse section through the colony base illustrating the early stages of backbudding and skeletal wall structure, Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 60$.

Fig. 6. Trepostome ancestrula. MSU 220314-00024c. An etched and polished section through the protoecium, ancestrula, and primary zooid of the same colony as illustrated in Pl. 127, fig. 6 showing details of wall structure, Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 400$.



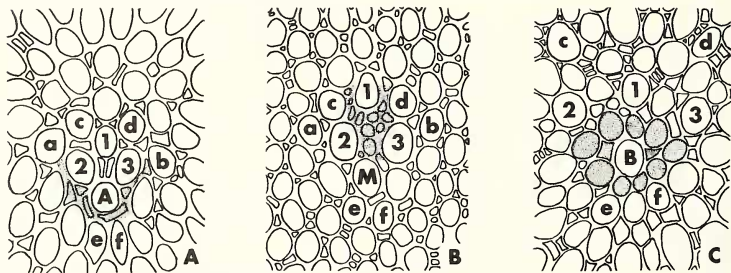
PODELL and ANSTEY, Bryozoan colonies

EARLY COLONY DEVELOPMENT

The growth of a stenolaemate bryozoan colony begins with the settlement of the founder zooid, the ancestrula. Initially the founder zooid grows parallel to the substrate, forming a tubular chamber constructed of external simple skeleton (Boardman and McKinney 1976) termed the protoecium. The zooid producing the protoecium is termed by Ryland (1970) the proancestrula. The proancestrula initially grows distally (along the substrate), but eventually turns upward (anteriorly) to become the ancestrula proper (orientation terminology from Gautier 1970). The protoecium may be separated from the ancestrula by a slight constriction, as in the genus *Prasopora* (Cumings 1912), or by a diaphragm, as in the genus *Rhombotrypa* (Boardman and McKinney 1976). In most Ordovician trepostomes there is no demarcation between the two, as in the genus *Hallopora* (Pl. 126, fig. 4).

The external simple skeleton of the proancestrula appears to differ crystallographically from the skeleton of subsequently formed parts of the colony. In what are most likely trepostome protoecia encrusting on *Rafinesquina* valves, the external surface of the skeleton consists of a fanlike cluster of proximally radiating elongate crystal units with sutured margins between crystals (Pl. 126, figs. 1-3; Pl. 127, fig. 1). As seen in etched sections (Pl. 126, figs. 4-6), however, the protoecial wall, although thinner, is constructed of multiple laminations identical to those in the wall of subsequently budded zooids.

The first generation of additional zooids is produced by asexual budding from the distal side of the ancestrula near the substrate (Pl. 126, fig. 4; Pl. 127, fig. 6). The primary zooids are those in contact with the distal wall of the ancestrula. *Rhombotrypa* has four primary zooids (Pl. 127, figs. 3, 4), whereas *Hallopora* (Pl. 130, fig. 2),



TEXT-FIG. 1. Comparison of the ancestrula, monarchozooid, and basilozooid. A, Ancestrular cluster with the region of the protoecial flange (shaded), ancestrula (labelled A), primary zooids (labelled 1-3), secondary zooids (labelled a-d), and backbudded zooids (labelled e and f), enlarged from Pl. 128, fig. 3. B, A monticule including the monarchozooid (labelled M), triangular central cluster of mesopores (shaded), and primary, secondary, and backbudded zooids (labelled as in A), from Pl. 129, fig. 3. C, A branch axis (from Pl. 129, fig. 1, rotated 180°) including the basilozooid (labelled B) and the ring of zooids (shaded) that originated from it; this basilozooid is histologically continuous with the ancestrula; original primary and secondary zooids labelled as in A and B, all $\times 18$.

Amplexopora? (Pl. 126, fig. 5; Pl. 128, fig. 2), *Homotrypa*? (text-fig. 1a; Pl. 128, figs. 3, 5), *Prasopora* (text-fig. 2), and thirteen unidentifiable early colonies (Pl. 127, fig. 6; Pl. 128, figs. 1, 4) have three.

The second generation of zooids buds distally from the primaries, and the third generation buds likewise from the secondaries, producing an initially triangular colony (Pl. 127, fig. 6) with the protoecium at its apex, termed the protoecial cone by Boardman and McKinney (1976). The shape of the protoecial cone is governed by the number of newly budded zooids produced per generation. Colonies with only a small increase in each generation form long isosceles triangles (Pl. 128, fig. 1), whereas an accelerated budding rate quickly enlarges the distal margin to produce subcircular colonies (Pl. 126, fig. 5). The latter type of development leads to the proximal displacement of the lateral sides of the growing margin, so that after only a few generations, zooids have filled in the region behind the ancestrula and form small circular colonies (Pl. 128, fig. 4). The proximal addition of later generation zooids that fill in the region behind the ancestrula will be referred to below as backbudding. In the development of the protoecial cone, some taxa produce more buds on one side of the growing margin than on the other, producing somewhat spiral protoecial cones that may be described as righthanded (Pl. 127, figs. 3, 4) or lefthanded colonies (Pl. 130, fig. 2).

At some early stage in the development of the protoecial cone, the proximal wall of the ancestrula and its laterally adjacent primary zooids becomes unusually thickened, forming a V-shaped 'flange' around the apex of the triangular colony (Pl. 127, figs. 4, 6), the lateral ends of which extend as processes protruding from the colony margin (Pl. 127, fig. 5). The apical flange does not overlap the protoecium, which still remains visible at this stage of development, projecting proximally from the centre of the flange. After backbudding has filled in the space behind the ancestrula, the flange remains observable as a V-shaped region of thickened wall (text-fig. 1a; Pl. 128, figs. 3, 4) within the early colony and its lateral edges may project into some zooecia (Pl. 127, fig. 5). This structure is particularly useful in identifying the ancestrula and the primary zooids in both early and somewhat later stages of colony growth (Pl. 128, figs. 2-5). This thickened wall region was previously observed in thin sections in the initial regions of fully developed colonies of four trepostome genera by Cumings (1912) and of two additional genera by Boardman and McKinney (1976) and McKinney (1977b). Scanning electron micrographs of this thickened region viewed longitudinally (Pl. 127, fig. 2) and transversely (Pl. 127, figs. 4, 5) indicate that the small crystals making up the wall laminae change from a vertical orientation on its distal margin to horizontal in the centre to vertical again on its proximal margin, demonstrating that the wall laminae are folded over in a proximally developed flexure. Boardman and McKinney (1976) attributed the same structure (a double layer of external simple skeleton on the proximal side of the ancestrula) in *Rhombotrypa* to a proximal flexure of the external colony wall down to the substrate. The thickened flange and its lateral projections could have been of functional importance to the early colony, possibly by restricting water flow and thereby improving the filter-feeding ability of the early formed zooids. Following the development of the protoecial flange, backbudding is accelerated at the expense of distal budding, so that colonies become subcircular with the ancestrula centrally located (Pl. 128, figs. 2-5). This stage

of development is termed herein the ancestrular disc. The loci and rates of subsequent budding determine the ultimate colony growth habit: peripheral budding produces sheetlike colonies (and variations thereof), whereas distal extensions of the internal zoecia and internal budding produce the series of mound to hemisphere to pillar to branching colony forms.

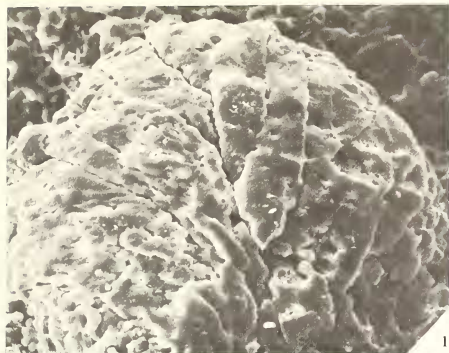
The development of morphogenetic gradients within the protoecial cone is variable. In both *Rhombotrypa* and *Hallopora* (Pl. 127, fig. 3; Pl. 130, fig. 2), the ancestrula is the smallest zooid in the early colony, and subsequent generations increase in size away from it, producing a positive morphogenetic size gradient. In the earliest stage of *Prasopora conoidea* (text-fig. 2a), however, the ancestrula is the largest zooid, and subsequent generations decrease in size away from it, producing a negative morphogenetic size gradient. Available data indicate, however, that all positive gradients disappear by the stage of the development of the ancestrular disc. All available ancestrular discs display either no obvious gradients (as in *Rhombotrypa*), or well-developed negative gradients leading away from the ancestrula (as in most of the taxa studied). This suggests that some colonies experienced a developmental change from positive allometry in the protoecial cone to negative allometry in the ancestrular disc.

The dominance of the ancestrula within the ancestrular disc is illustrated by the orientation of cystiphragms in monticuliporid genera (Pl. 128, figs. 2, 5; text-fig. 2a). In addition to their radial development of morphogenetic gradients, the cystiphragms in each zoecium are radially aligned with the ancestrula. Identical radial alignment of cystiphragms is developed around monticuliporid monticules (Boardman and Utgaard 1966), and is probably related to the inferred function of monticules as excurrent water outlets (Anstey *et al.* 1976).

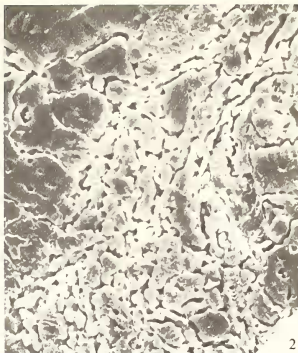
Furthermore, the ring of zooids immediately surrounding the ancestrula in many colonies becomes differentiated from the other zooids of the disc to form the first monticule (polymorphic cluster) of the early colony (text-fig. 2b). Commonly the primary and secondary zooids of the protoecial cone (still observable because of the thickened wall area of the apical flange) become as large as the ancestrula, and many small newly budded zooids produced from the distal side of the ancestrula displace the large

EXPLANATION OF PLATE 127

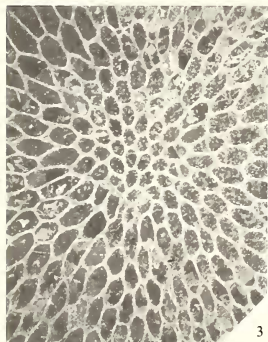
- Fig. 1. Trepostome protoecium. MSU 220314-00024b. Enlargement of protoecium on left in Pl. 126, fig. 3, illustrating the radial orientation of crystal units, Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 630$.
- Fig. 2. *Hallopora* sp. MSU 220314-00090. Enlargement of thickened region on the left side of the ancestrula and protoecium of Pl. 126, fig. 4 (reversed image), illustrating wall structure within the protoecial flange, Madison, Indiana, Dillsboro Formation (Late Ordovician), $\times 1000$.
- Figs. 3-5. *Rhombotrypa* sp. MSU 220314-00030. Versailles, Indiana, Dillsboro Formation (Late Ordovician). 3, tangential section through the colony base showing a positive morphogenetic gradient, $\times 20$. 4, enlargement of initial region of fig. 3 displaying four primary zooids, ancestrula, and thickened wall, $\times 180$. 5, enlargement of lower right-hand corner of fig. 4, illustrating the flange of the thickened wall protruding into the right-hand most primary zooid, $\times 360$.
- Fig. 6. Trepostome protoecial cone. MSU 220314-00024c. Early astogeny illustrating the external wall of the protoecium, thickened backwall, protruding flange, and primary zooids, Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 100$.



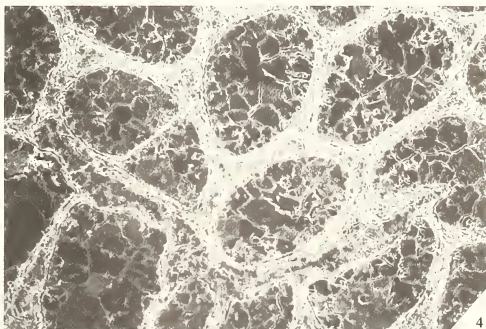
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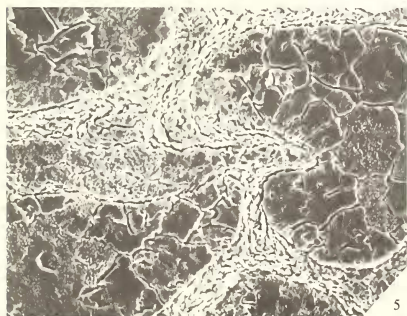
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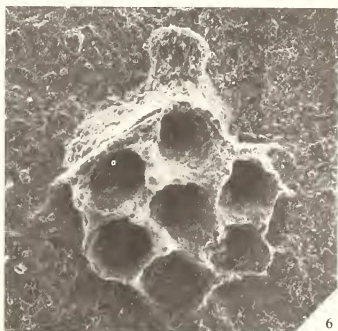
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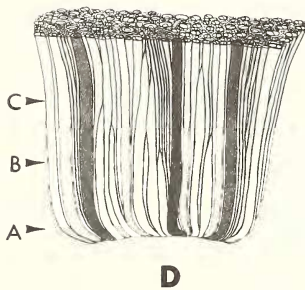
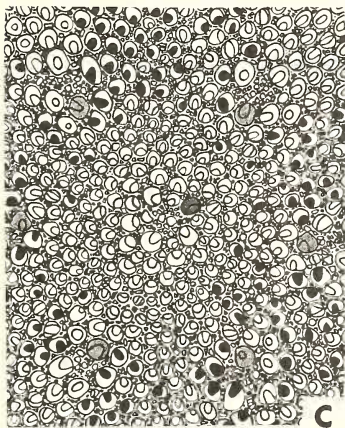
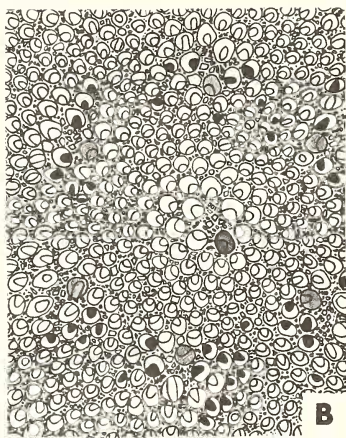
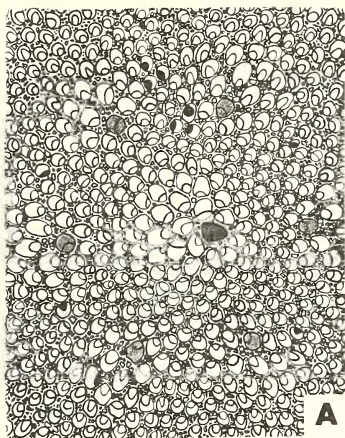
zooids away from the ancestrula, so that a ringlike structure is developed (text-fig. 2*b, c*). Most trepostome monticules include a central cluster of very small zooids (Pl. 129, figs. 3, 4). With the appearance of the first monticule, early colony development is complete.

DEVELOPMENT OF MONTICULES

The second stage of colony development involves the differentiation of additional monticules as the colony grows peripherally. New monticules appear at regular distances from the ancestrular cluster (the original monticule) and from each other. In *Prasopora conoidea* (text-fig. 2*a*) new monticules arise at regular intervals of approximately 1 cm. The key developmental aspect of monticules is their nearly exact duplication of the ancestrular cluster, complete with a replicated ancestrula, primary and secondary zooids, and vestiges of the protoecial cone. In addition they display dominance effects over their region of the colony (which incorporates about 200 or so extramonticular autozooids) identical to the dominance of the ancestrula over the ancestrular disc. Large sheetlike colonies (or the exozonal surfaces of monticulated colonies having other growth forms) are in fact simple aggregates of hexagonally arranged monticular subcolonies that each replicates the ancestrular disc. Because each subcolony is developed within the spatial constraints imposed by neighbouring subcolonies, their boundaries cannot be circular like that of the ancestrular disc, but become nearly hexagonal (Anstey *et al.* 1976). The dominance effects of monticules are shown by their location at the centre of radially developed morphogenetic gradients within subcolonies and, in certain taxa, radial alignment of cystiphragms or lunaria.

In the ancestrular cluster the backbudded zooids (*e* and *f* in text-fig. 1*a*) are separated from the ancestrula and the primary zooids (A, and 1, 2, and 3) by the thickened wall region that remains from the apical flange of the protoecial cone, thus preserving the triangular structure of an earlier stage of development. In monticules the ancestrular replicate, the monarchozooid (Anstey and Pachut 1977), is likewise at the apex of a triangular structure formed by the secondary zooids and central cluster of small zooids (text-figs. 1*b, 2d*; Pl. 129, figs. 3, 4), although in monticules there is no V-shaped region of thickened wall. In monticules, very small

TEXT-FIG. 2. Dominance effects in the early development of *Prasopora conoidea* Ulrich. MSU 220323-00001. A, Transverse section cut at the colony base illustrating the radial disposition of cystiphragms and negative morphogenetic gradients centred on the ancestrula (shaded dark grey). Monarchozooids are shaded light grey, and zooids in which the cystiphragms point away from the ancestrula are coloured solid black. B, Transverse section approximately 0.5 mm above the colony base showing the increase in the number of cystiphragms that have become reoriented around their respective monticules and the increase in the number of small zooids within the ancestrular and monticular clusters. C, Transverse section approximately 1.0 mm above the substrate showing the continuation of cystiphragm reorientation and the distal spread and enlargement of the clusters of small zooids, all $\times 27$. D, A three-dimensional reconstruction of the central portion of the colony base (approximately 1.5 mm high) from serial acetate peels illustrating the budding of small zooids (shaded light grey) from the ancestrula (shaded dark grey) and from two monarchozooids (shaded medium grey), Cannon Falls, Minnesota, Decorah Shale (Middle Ordovician), $\times 12$.

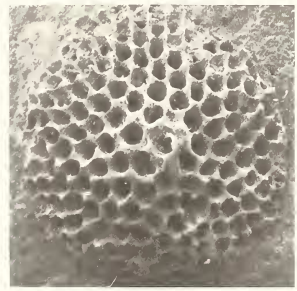
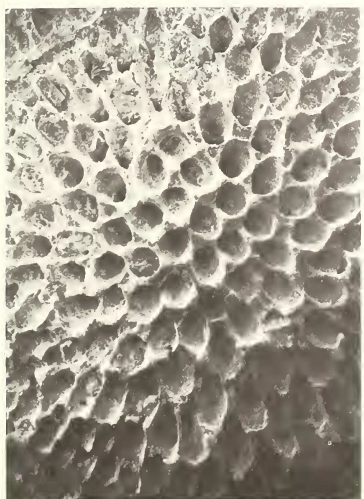
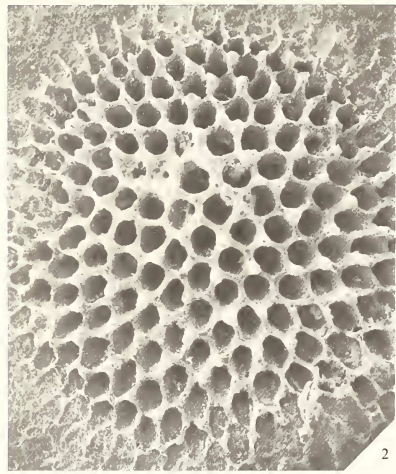


zooids (probably polymorphic) are budded from the distal side of the monarchozooid, and form a central cluster that is generally triangular in shape (shaded region in text-figs. 1*b* and 2*d*). In the ancestral cluster, the small zooids displace the primary zooids distally, as Cumings (1912) illustrated in *Prasopora conoidea*. In colonies with three primary zooids, the large zooid opposite the monarchozooid and separated from it by the small zooids in a monticule is a replicate of the median primary zooid of the early colony. The central cluster of small zooids commonly bifurcates around the median primary, thus forming a U-shaped structure on the distal side of the monticule and imparting to the monticule an additional element of bilateral symmetry. In many monticules the small central zooids increase in size from the monarchozooid to the median primary zooid (Pl. 130, figs. 1, 3) suggesting that continued budding within the monticule leads to the formation of a succession of median primaries, with the older ones displaced into the monticular border. This size gradient within the monticule itself duplicates the positive morphogenetic gradient observed in the protoecial cones of *Hallopora* and *Rhombotrypa* (Pl. 130, fig. 2; Pl. 127, fig. 3). In the genus *Hallopora* the median primary zooid of monticules is particularly distinctive because it is floored by a very shallow diaphragm (Pl. 129, fig. 3). In most taxa the large monticular polymorphic zooids form a complete ring around the central cluster of small zooids. The monarchozooid is usually located inside the outer ring of large polymorphs slightly into the central cluster of small zooids (text-fig. 1*b*), whereas the median primary zooid is usually well within the central cluster, and may be completely surrounded by small zooids. Outside the monticule the nonpolymorphic autozooids gradually decrease in size in a negative gradient extending from the monticular border to the subcolony boundary. To date we have identified distinctive monarchozooids in the monticules of fifteen Palaeozoic genera representing seven families.

In the family Monticuliporidae cystiphragms are generally radially arranged around the monticules (Boardman and Utgaard 1966). In some genera the cystiphragms point towards the monticule, as in *Prasopora*, but in others away from it, as in *Monticulipora*. These arrangements suggest the developmental dominance of the monarchozooid over its own subcolony. Subcolony maps can be prepared by drawing their boundaries at the places where cystiphragms reverse their orientation. The dominance

EXPLANATION OF PLATE 128

- Fig. 1. Trepostome protoecial cone. MSU 220314-00046a. Colony with a large number of distal zooids; protoecium is in the upper centre of the micrograph, Madison, Indiana, Dillsboro Formation (Late Ordovician), $\times 75$.
- Fig. 2. *Amplexopora?* sp. MSU 220314-00027b. Ancestrular disc with its centrally located ancestrula and protoecial flange, Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 35$.
- Figs. 3, 5. *Homotrypa* sp. Versailles, Indiana, Dillsboro Formation (Late Ordovician). 3, MSU 220314-00028a. Ancestrular disc illustrating the ancestrula (distal to thickened wall area) surrounded by cystiphragms oriented towards it, $\times 35$. 5, MSU 220314-00028b. Ancestrular disc illustrating similar features to those in fig. 3, $\times 35$.
- Fig. 4. Ancestrular disc. MSU 220314-00027c. Note the thickened wall around the ancestrula and negative morphogenetic gradient in peripherally spreading zooids, Versailles, Indiana, Dillsboro Formation (Late Ordovician), $\times 25$.



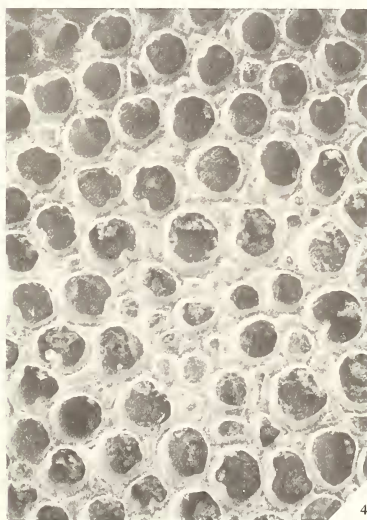
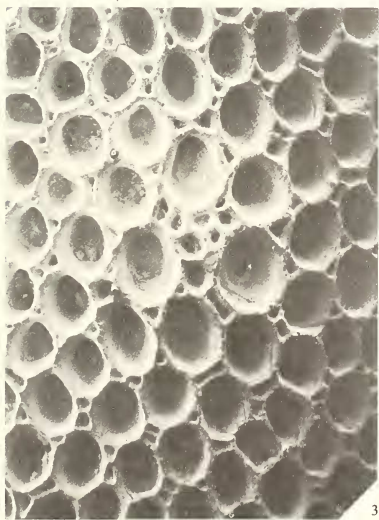
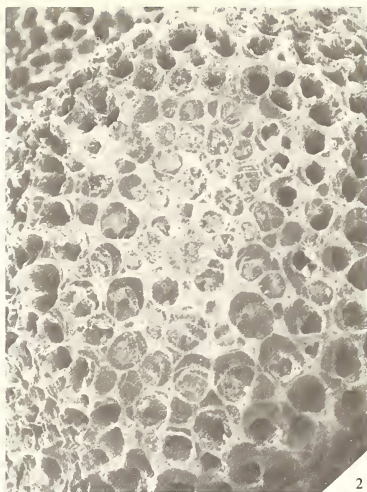
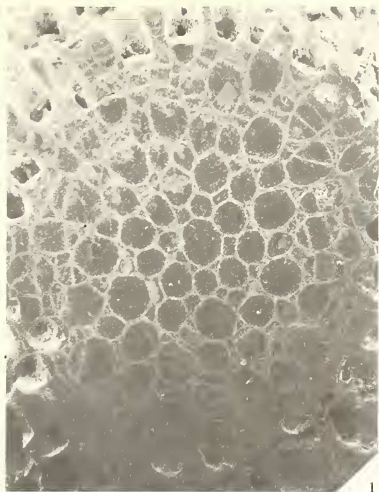
PODELL and ANSTEY, Bryozoan colonies

of the monarchozooid over these patterns is confirmed by observations of areas damaged by boring organisms in *Prasopora simulatrix*. In undamaged subcolonies the radial alignment of the cystiphragms is well developed, but in the adjacent regions affected by the borings, no monticules are observable and the cystiphragms are randomly oriented. Presumably the loss of the monarchozooids to the borers resulted in a local absence of the developmental regulation. This example provides additional support for the hypothesis advanced elsewhere (Anstey *et al.* 1976; Pacht unpublished thesis, Michigan State University 1977) that bryozoan subcolonies were regulated by the diffusion of a morphogenetic substance released from the monarchozooid. Such regulation is possible in trepostome bryozoans because of interzooidal communication via a common colonial coelom and hypostegal cell layers (Boardman and Cheetham 1973).

The post-ancestrular disc development of *P. conoidea* documents the transfer of local dominance from the ancestrula to the newly differentiated monarchozooids in the peripheral regions of the colony. Serial sections taken from the lowest levels within the colony show that the cystiphragms are not initially radially aligned with their local monticules, but are all pointing towards the ancestrula (text-fig. 2a). Higher sections show that the zooids nearest each monticule are the first to turn away from the ancestrula and towards the local monarchozooid, and that the realignment progresses as 'waves' that spread radially from the monticular centers (text-fig. 2b). At the height of 1 mm above the substrate, all of the zooids have become incorporated into local subcolonies, each dominated by a monarchozooid and the only zooids still aligned with the ancestrula are those in its local subcolony (text-fig. 2c). This evidence suggests that zooid alignment is regulated by a morphogenetic substance produced initially by the ancestrula and diffused outward into the colony. Subsequently newly differentiated monarchozooids begin to produce the same substance which gradually increases in concentration radially away from each, thereby spreading the zones of local dominance until the early colony is completely subdivided into such zones.

EXPLANATION OF PLATE 129

- Fig. 1. *Hallopora* sp. MSU 220314-00052. Transverse section through a pillar-shaped colony displaying an enlarged, centrally located basilo zooid surrounded by several new zooids (rotated 180° from text-fig. 1c), Madison, Indiana, Dillsboro Formation (Late Ordovician), $\times 40$.
- Fig. 2. *Homotrypella hospitalis* (Nicholson). MSU 220314-00055. Transverse section through a branch illustrating the centrally located enlarged basilo zooid encircled by newly budded zooids, Madison, Indiana, Dillsboro Formation (Late Ordovician), $\times 30$.
- Fig. 3. *Hallopora* sp. MSU 220314-00019. Monticular polymorphic cluster illustrating the monarchozooid (below central cluster of mesopores) and median primary zooid (above central cluster of mesopores), West Harrison, Indiana, Eden Shale (Late Ordovician), $\times 35$.
- Fig. 4. *Peronopora* sp. MSU 220314-00017. Monticule showing the monarchozooid (very bottom of micrograph) and the median primary zooid (centre of micrograph at upper end of central cluster of mesopores), West Harrison, Indiana, Eden Shale (Late Ordovician), $\times 35$.



DEVELOPMENT OF BRANCHES

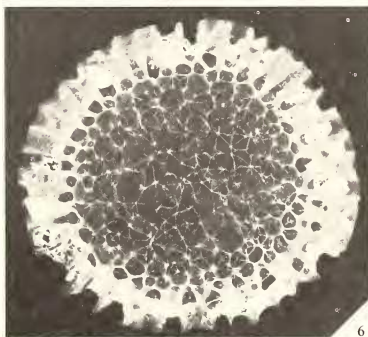
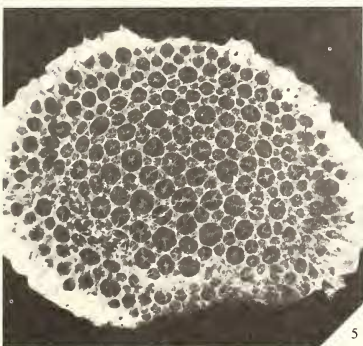
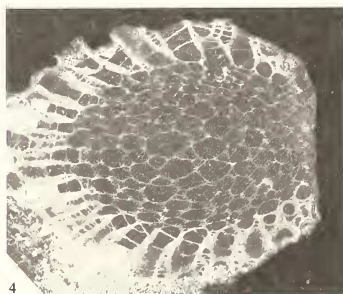
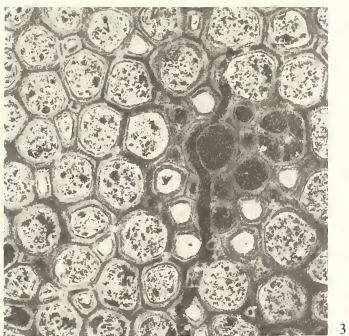
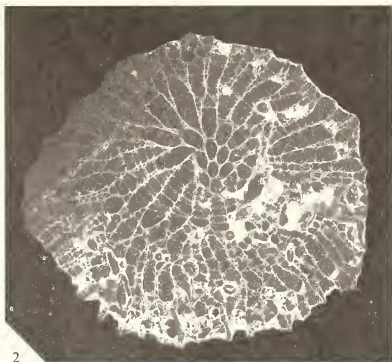
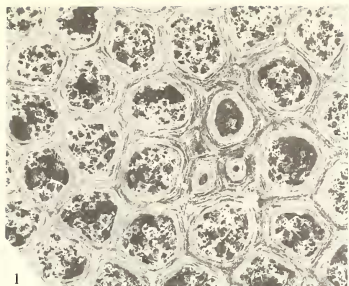
Cumings (1912) suggested that the development of colony branches could be related to that of monticules, and Blake (1976) effectively illustrated the developmental interrelationship of branches and monticules in the genus *Rhabdomeson*. Branching colonies, however, commonly have two developmental zones: an inner (axial) zone of long, vertically oriented thin-walled undifferentiated zooecia, termed the endozone, and an outer (cortical) zone of short, thick-walled zooecia with a variety of intra-zooecial and extra-zooecial structures, the exozone. Even massive and hemispherical colonies may have cyclic repetitions of laminar growth zones that vary from endozonal to exozonal characteristics. Monticules are developed only within the exozone, and the regulation of exozonal characteristics is related to the morphogenetic gradients associated with monarchozooids. This study seeks to demonstrate that a second type of ancestral replicate, the basilo zooid (Anstey and Pachut 1977), is found within the axial zones of colony branches, and may be involved in the regulation of endozonal development.

Large axial zooids are present in the endozones of many Palaeozoic branching colonies (Pl. 129, figs. 1, 2; Pl. 130, figs. 4-6), which are probably basilo zooids. Unusually large axial zooids are also present in a number of post-Palaeozoic cyclostomes (Nye 1976). In addition to large size, general characteristics of basilo zooids include central or near central location, vertical continuity within the branch axis, and location at the origin of radial morphogenetic gradients in size, shape, zooecial structure, and budding. It is also possible that some taxa have functional basilo zooids that are not morphologically distinctive. To date we have identified distinctive basilo zooids in twenty-one Palaeozoic genera representing ten families.

The processes leading to branch bifurcation are incompletely known, but new branches may arise from an expansion of the axial endozone and the differentiation

EXPLANATION OF PLATE 130

- Fig. 1. *Amplexopora septosa* (Ulrich). Indiana University, 8979-17005. Tangential section through a monticule showing the monarchozooid (centrally located in lower half of micrograph) and enlargement in new zooids as they are displaced distally away from it, Miamitown, Ohio, Eden Shale (Late Ordovician), $\times 40$.
- Fig. 2. *Hallopora dalei* (Milne-Edwards & Haime). Indiana University, 9106-23. Transverse section through the colony base illustrating the positive morphogenetic gradient radiating away from the centrally located ancestrula, near Guilford, Indiana, Dillsboro Formation (Late Ordovician), $\times 35$.
- Fig. 3. *Heterotrypa ulrichi* (Nicholson). Indiana University, 8976-25007. Tangential section through a monticule illustrating the distal spread and enlargement of new zooids from the monarchozooid, Miamitown, Ohio, Eden Shale (Late Ordovician), $\times 40$.
- Fig. 4. *Hallopora nodulosa* (Nicholson). Indiana University, 8974-15005. Transverse section through a branch showing the enlarged, centrally located basilo zooid and negative morphogenetic gradient radiating away from it, Gallatin County, Kentucky, Eden Shale (Late Ordovician), $\times 35$.
- Fig. 5. *Hallopora ramosa* (D'Orbigny). Indiana University, 9004-13. Transverse section taken through a branch displaying the centrally located basilo zooid and negative morphogenetic gradient radiating away from it, near Guilford, Indiana, Dillsboro Formation (Late Ordovician), $\times 35$.
- Fig. 6. *Eridotrypa simulatrix* (Ulrich). Indiana University, 9135-14. Transverse section cut through a branch illustrating centrally located, enlarged basilo zooid, near Guilford, Indiana, Dillsboro Formation (Late Ordovician), $\times 35$.



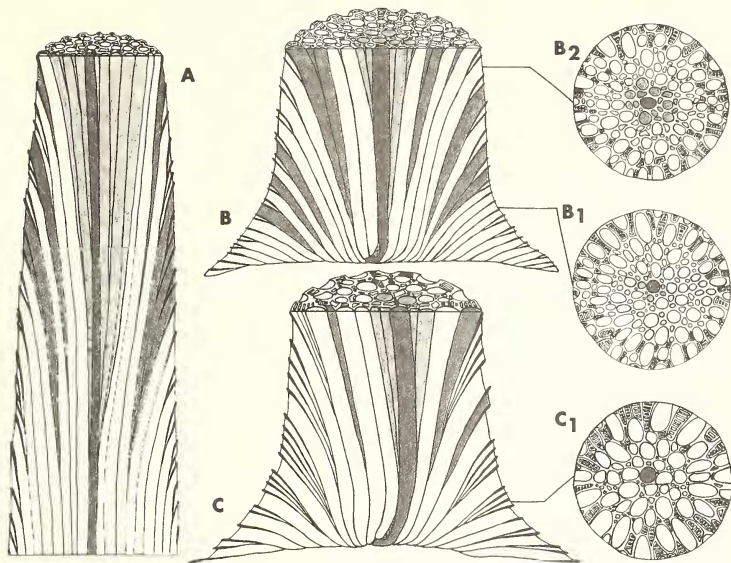
of a second basilozoid, just as new monticules develop as a distance effect with respect to previous ones. A transverse section of *Leptotrypella pellucida* has two separate basilozooids in an expanded endozone, suggesting that branch bifurcation is a result of the duplication of the axial monarch. Some branching and frondescent colonies have small warty protuberances capped by a monticule, suggesting that some branches may have developed directly from a monticule. Whether or not the development of a branch can cause absorption of previously existing exozonal skeleton is presently unknown. More complex developmental processes than those described above must have been involved in the growth of frondescent and anastomosing colonies. Because basilozooids can only be studied by the laborious method of serial sectioning, very little is presently known about them, and further development of these ideas must await more research.

After the stage of the ancestrular disc, some colonies grow upward from the substrate by vertical extension of the zooecial tubes instead of lateral extension of the colony by marginal budding. Such colonies initially become a hemispherical mound 2 or 3 mm high, which subsequently becomes attenuated into a pillar. The region of upward growth is centred on the ancestrula, which continues up the branch axis as a centrally located zooid (text-fig. 3). The vertical continuity of this zooid in the branch axis is determined by the superposition of very closely spaced acetate peels, and usually cannot be observed directly in longitudinal sections because of the displacement of individuals in and out of the place of section caused by budding. This zooid, the basilozoid, is histologically continuous with the ancestrula, is centred within the endozone, and exozonal differentiation occurs at uniform distances from it. In the genus *Hallopora* (text-fig. 3), new buds develop on all sides of the basilozoid, and gradually displace the original primary and secondary zooids outwards by newer buds so that the new buds collectively form an inverted axial cone centred on the basilozoid that expands in diameter up the branch (text-figs. 1c, 3a). Although the original basilozoid in *Hallopora* is more vertically extensive than any other zooid, in some colonies even it is eventually displaced into the exozone and is replaced in the branch axis by a secondary basilozoid.

A hemispherical colony of *Homotrypella hospitalis* (Pl. 129, fig. 2) produced a small pillarlike protuberance on the margin of the colony. Within this structure, which resembles an early stage in branch development, a large axial zooid is not only centrally located, but the cystiphragms of all the surrounding zooids are radially aligned with it. This structure is a true intermediate stage between a monticule and a branch. Transition series may exist among all three types of monarchic zooids.

CONCLUSIONS

Early colony development, as observed in Ordovician trepostome bryozoans, consists initially of distal budding from the ancestrula along the substrate, forming a flat triangular colony in which a positive morphogenetic gradient may be present. The completion of backbudding forms a circular colony, the ancestrular disc, characterized by negative morphogenetic gradients leading away from the ancestrula. Subsequent growth may be marginal, by means of budding along the substrate, and/or upward, by vertical extension of the colony centre. Colony surfaces develop regularly posi-



TEXT-FIG. 3. Development of colony branches in the astogeny of *Hallopora* spp.; longitudinal sections reconstructed from serial acetate peels. A, MSU 220314-00089. A colony branch illustrating the centrally located basozooid (shaded dark grey), zooids originating directly from it (shaded light grey), and zooids originating from other parts of the endozone (shaded medium grey), West Harrison, Indiana, Eden Shale (Late Ordovician). B, MSU 220314-00052. Pillarlike colony illustrating the continuation of the ancestrula as a basozooid (shaded dark grey), and budding of new zooids (shaded light grey) from the basozooid. Transverse sections B_1 and B_2 illustrate the basozooid (dark grey) and buds originating from it (light grey) at two levels within the colony, Madison, Indiana, Dillsboro Formation (Late Ordovician). C, MSU 220314-00067. Longitudinal view of pillarlike colony with similar additions of new zooids to that of A and B. Transverse section C_1 illustrates a very early stage in the budding of new zooids from the basozooid, Miamitown, Ohio, Eden Shale (Late Ordovician), all $\times 17$.

tioned polymorphic clusters, or monticules, in which the monarchozooid replicates the ancestrula and is inferred to have maintained negative morphogenetic gradients to the margin of the monticular subcolony. Branch axes also contain an ancestral replicate, the basizooid, which may also have maintained morphogenetic gradients within the axial endozone. From these observations it may be concluded, as interpreted in the light of possible growth regulation, that the early development of a colony reflects a developmental programme which has a substantial effect on all later stages of colony growth.

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